The Influence of Opponent-Related and Outcome-Related Memory on Repeated Aggressive Encounters in the Paradise Fish (*Macropodus opercularis*)

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Abstract. The aggressive behavior of male paradise fish (*Macropodus opercularis*) was studied. Fish were subjected to three aggressive encounters on consecutive days. If submissive males encountered the same opponent three times, the last aggressive encounter was very different than the first one. When the animals faced a new opponent each day, the changes were much less pronounced. We conclude that (1) fish are able to recognize their opponents at least one day after the encounter ("social recognition"), and (2) social recognition modifies the effect of prior defeat ("status-related memory") in subsequent encounters.

Introduction

An overwhelming amount of evidence indicates that prior agonistic experience influences the outcome of future aggressive encounters (Beacham and Newman, 1987; Frank and Ribowsi, 1987). One can hypothesize that prior aggressive experience may influence subsequent aggressive encounters by two kinds of processes: one related to the outcome of the encounter ("winner" or "loser" effect) and the other specifically related to the opponent. The significance of the former process was recently examined in detail (Bevan *et al.*, 1960; Poll *et al.*, 1982; Francis, 1983; Beaugrand and Zayan, 1985; Beacham and Newman, 1987; Bakker *et al.*, 1989). Most studies demonstrate an asymmetrical effect of prior winning or losing on subsequent winning probability. For example, in paradise fish (*Macropodus opercularis;* Francis, 1983) and in sticklebacks (*Gasterosteus aculeatus;* Bakker and Sevenster, 1983) losing greatly enhances the probability of also losing

the subsequent contest. Winning usually has no strong effect, but under some experimental conditions it might increase the probability of winning again (Bakker and Sevenster, 1983; Bakker *et al.*, 1989).

The possibility of the involvement of the second process—individual recognition—in agonistic encounters has been also demonstrated. Fricke (1973) showed that *Amphiprion bicinctus* males more frequently attacked unknown individuals than known ones in a two-choice experiment. The importance of individual recognition in the stickleback was demonstrated by Peeke and Veno (1973), who observed that a resident male that had been habituated to an intruder presented in a glass cylinder would resume aggressive behavior if the individual in the cylinder was changed. Thresher (1979) used a similar method to study rival recognition in the threespot damselfish (*Eupomaceus planifrons*), and those field observations further confirm that some fish species might be able to recognize individuals. Myrberg and Riggio (1985) showed that coral reef fish (*Pomacentrus partitus*) recognize territorial neighbors acoustically. Recently Waas and Colgan (1994) provided experimental evidence that male sticklebacks can distinguish between familiar rivals on the basis of visual cues alone.

Assuming that the effects of previous encounters are mediated by memory—and that the behavioral differences are not due to energetic consequences of aggression (Haller and Wittenberger, 1988; Haller, 1991)—the problem of interference between social recognition and status-related memory arises.

As a continuation of a recent study (Miklósi *et al.*, 1992) on aggressive behavior in the paradise fish, we experimentally examined these processes in the aggressive behavior of the paradise fish. To clarify the relationship be-

tween social recognition and status-related memory, two questions have been posed: (1) Does the behavior of the fish change if it encounters the same or different opponents for two subsequent encounters? (2) Are there differences between these experimental manipulations?

Materials and Methods

Experiments were conducted with 6-month-old, 8-cm to 10-cm-long *Macropodus opercularis* males, which were raised and kept in our laboratory. Three days before the start of the experiment, pairs of size-matched fish were placed in 40 × 20 × 20 cm glass tanks provided with filtration and aeration. Each tank was separated into two equal parts by a green opaque screen, and a single fish was kept in each part of the tank. The animals were visually isolated from each other: all sides but the front side of the tanks were covered with green plastic sheets. This isolation lasted 3 days prior to the experiment. Water temperature was kept at 28°C, and a 14:10 h light:dark cycle was maintained. The fish were fed daily on *Tubifex* worms.

Animals were exposed to three aggressive encounters on successive days. Encounters were begun by removing the plastic partition. All encounters were videotaped until dominance relationships were established. We defined this as the point at which one of the fighting males no longer participated in simultaneous or reciprocal threatening and fighting but instead became the "subordinate," showed fleeing and escaping behavior when approached by the "dominant," which in turn chased and bit its opponent. A submissive fish remains motionless for a long time in "oblique position" near to the water surface and does not retaliate against the winner (Miklósi *et al.,* unpub. obs.; Forselius, 1957). Both fish were observed for an additional hour to monitor the stability of the dominant-subordinate relationship. One hour after the end of fighting, the contact between the fish was interrupted by lowering the plastic door, and the animals were kept in isolation for the next 24 h.

Two groups were tested: the fish in group A (*n* = 10) faced the same opponent throughout the experiment; in group B (*n* = 10) the dominant animals were randomly changed between the tanks after each fight. Thus, in group B, the submissive fish remained in the tank and faced a new, previously dominant opponent each day. The dominant fish was changed immediately after the end of the encounter and remained isolated in its new tank until the following day when the partition was removed again. The time between two consecutive encounters was long enough for the dominant to acclimate to the new place (Csányi *et al.,* 1985), thus the advantage of prior residency of the submissive fish was minimized.

Videotapes were later analyzed by recording behavioral units with an event recorder (Nagy *et al.,* 1985). On the

basis of earlier findings, each aggressive encounter was divided into three main phases: latency, threatening, and fighting. After the latency for initiation of the first display, a second phase was defined, which lasted until the first appearance of contact behavior (biting or mouthlocking). This was called threatening, which in turn was followed by the escalation of the fighting—fighting phase—until one of the males showed submissive behavior. The behavior units we identified are as follows:

Display at distance (DIS): The fish stay in head-tail position with erected tailfin, but the distance between them is larger then one body length.

Head-head display (HHD): The fish are oriented parallel to one other and face in the same direction, with one fish slightly behind the other.

Parallel swimming (PAS): The fish swim very close to each other in the same direction.

Head-tail display (HTD): The fish in parallel orientation are facing opposite directions. Sometimes this behavior is associated with circling.

Shaking (SHA): This behavior is similar to the head-tail display, but it is associated with fast circling, vigorous body-shaking, and a downward movement of the pair; the pattern stops when the animals reach the bottom.

Bite (BIT): One fish makes a swift dart and slashes at the other fish.

Mouthlock (MOU): The fish reciprocally bite and hold one another's mouths for up to 2 min.

Air gulping (AG): A fish takes an air bubble in its mouth by breaking the surface of the water.

Each of these behavioral units was recorded in all of the pairs investigated. Two samples of behavior were registered. The first sample, which characterized behavior during the threatening phase, lasted for 10 min from the raising of the door or until the first instance of contact behavior (biting or mouthlocking). The second sample, which characterized the fighting phase, was a 20-min observation following the first observed bite.

To permit comparison between pairs, the values of observed behavior units were divided by the sampling time. This adjustment was necessary because in many contests fish finished the threatening or fighting phase before our predetermined interval (10 or 20 min) of observations ended, resulting in shorter time samples. Thus the relative duration (minutes per hour) or frequency (number per minute) of behavior units was used for statistical analysis.

Because the measured variables were not normally distributed (according to the Kolgomorov-Smirnov test), nonparametric statistical methods were used. Kruskal-Wallis's one-way ANOVA was used separately for groups A and B to examine the change in the general pattern of aggressive behavior.

Results

The difference between the two groups—that is, the different effects of the "treatments"—can be seen in Table I.

Repeated encounters with the same opponent, group A, caused marked change in aggressive behavior. Although the duration of the threatening phase did not change significantly in the course of the three encounters, shaking and air-gulping were significantly reduced. All measured variables (with the exception of head-head display) of fighting, including its duration, decreased significantly when submissive fish faced the same opponent three times.

Interestingly, the changes in the other group (B) were much less pronounced. When the submissive fish repeatedly faced new opponents, only minor changes could be observed in their aggressive behavior. The threatening phase did not change significantly; only the relative duration of shaking and the frequency of biting showed a marked decrease.

A comparison with current literature showed that some behavioral elements and parameters are of special importance. Thus head-tail display (*e.g.*, Baerends and Baerends-Van Roon, 1950; Barlow, 1962; Enquist and Jakobsson, 1986), biting (*e.g.*, Peeke and Veno, 1973; Frank *et al.*, 1985; Enquist and Jakobsson, 1986; Halperin and Dunham, 1994), mouthlocking (*e.g.*, Baerends and Baerends-Van Roon, 1950; Enquist and Jakobsson, 1986), duration of threatening (*e.g.*, Frank *et al.*, 1985), and duration of fighting (*e.g.*, Enquist *et al.*, 1990; Haller, 1992)

were examined further when we used the nonparametric Mann-Whitney test to compare the behavior of the two groups in the first, second, and third encounters (Fig. 1).

The two groups did not differ in the first and second encounter; however, with the exception of head-tail display, they differed markedly in the third encounter. The time spent with mouthlocking ($z = -2.4$, $P < 0.02$), the number of bites ($z = -2.3$, $P < 0.02$), and the duration of threatening ($z = -2.6$, $P < 0.01$) and fighting ($z = -1.9$, $P < 0.05$) were lower in the group (A) with the same opponent than in the group (B) with different opponents.

The same variables were compared by the nonparametric Wilcoxon test to show within-group differences during the three encounters. In group A—same opponent in each encounter—we found a significant change from the first to the second encounter only in fighting duration ($z = -2.8$, $P < 0.01$). However, significant changes occurred between the second and the third encounters in all of the selected variables (head-tail display: $z = -2.8$, $P < 0.01$; mouthlocking: $z = -2.6$, $P < 0.01$; biting: $z = -2.8$, $P < 0.01$; threatening: $z = -2.5$, $P < 0.02$; fighting: $z = -2.1$, $P < 0.04$). In contrast, no significant differences could be found in the group (B) with unknown opponents.

Discussion

The results clearly show that the type of opponent (familiar *versus* nonfamiliar) has a major effect on the aggressive behavior of male paradise fish. In the case of familiar opponents (group A), three consecutive encounters

Table I

Analysis of elements of aggressive behavior shown by fighting paradise fish pairs during three consecutive contests in both groups

	Group A: familiar opponent					Group B: unfamiliar opponent				
	encounter 1 Mean (SE)	encounter 2 Mean (SE)	encounter 3 Mean (SE)	Chi	Signif.	encounter 1 Mean (SE)	encounter 2 Mean (SE)	encounter 3 Mean (SE)	Chi	Signif.
Dur. of threatening	12.6 (2.1)	13.4 (2.9)	5.5 (1.8)	4.7	ns	12.3 (1.9)	12.1 (2.2)	11 (2.2)	1.7	ns
Head-head display	2.3 (0.9)	2.5 (0.7)	3.7 (1.4)	0.02	ns	4.4 (0.8)	6.2 (1.6)	3.6 (0.8)	0.7	ns
Shaking	2.3 (0.6)	1.7 (0.4)	0.4 (0.2)	7.3	$P < 0.03$	2.1 (0.7)	1.4 (0.3)	1.1 (0.3)	0.8	ns
Air-gulping	1.7 (0.4)	1.9 (0.7)	0.3 (0.1)	10.5	$P < 0.01$	3.2 (1.4)	1.9 (0.8)	2.5 (0.6)	2.5	ns
Parallel swimming	1.4 (0.7)	3.5 (1.3)	0.7 (0.3)	2.5	ns	2.1 (0.6)	4.4 (1.6)	1.6 (0.6)	2.1	ns
Head-tail display	32.2 (4.5)	36.1 (6.6)	19 (4.7)	4.7	ns	28.7 (4.4)	25.5 (5.1)	26.5 (4.3)	0.4	ns
Display at distance	4.1 (1.3)	3.1 (0.7)	5.1 (1.9)	0.2	ns	5.5 (1.8)	6.9 (3.5)	6.3 (2.1)	0.2	ns
Dur. of fighting	142.6 (40.1)	59.8 (22.8)	7.3 (3.5)	18.1	$P < 0.01$	115 (42.4)	50.1 (16.5)	54.8 (32.7)	4.9	ns
Head-head display	1.9 (0.8)	1.8 (0.8)	2.1 (1.4)	4.7	ns	4.4 (0.8)	6.2 (1.7)	3.6 (0.8)	0.1	ns
Shaking	1.3 (0.5)	1.2 (0.5)	0.5 (0.4)	5.9	$P < 0.01$	1.3 (0.2)	0.5 (0.2)	0.5 (0.2)	9.2	$P < 0.01$
Air-gulping	3.4 (0.9)	1.7 (0.5)	0.4 (0.3)	15.1	$P < 0.01$	3.1 (0.6)	2.6 (0.9)	1.6 (0.6)	4.0	ns
Parallel swimming	22.4 (6.2)	16.2 (5.7)	12.3 (2.8)	8.8	$P < 0.01$	20.4 (7.9)	3.1 (1.4)	2.5 (0.4)	0.9	ns
Head-tail display	39.6 (2.6)	31.4 (3.2)	10 (5.2)	8.8	$P < 0.02$	32.8 (2.2)	22 (5.5)	17 (5.4)	0.2	ns
Biting	1 (0.2)	1.1 (0.2)	0.1 (0.1)	15.3	$P < 0.01$	1.6 (0.3)	0.9 (0.3)	0.9 (0.3)	16.9	$P < 0.01$
Mouthlocking	13.8 (2.5)	9.2 (3.4)	0.8 (0.8)	17.3	$P < 0.01$	9.1 (1.8)	6.1 (2.4)	5.9 (2.2)	3.3	ns

Note: As a summary of the results, the mean (standard error) and the result of the one-way Kruskal-Wallis ANOVAs are given. The level of significance was greater than 0.05.
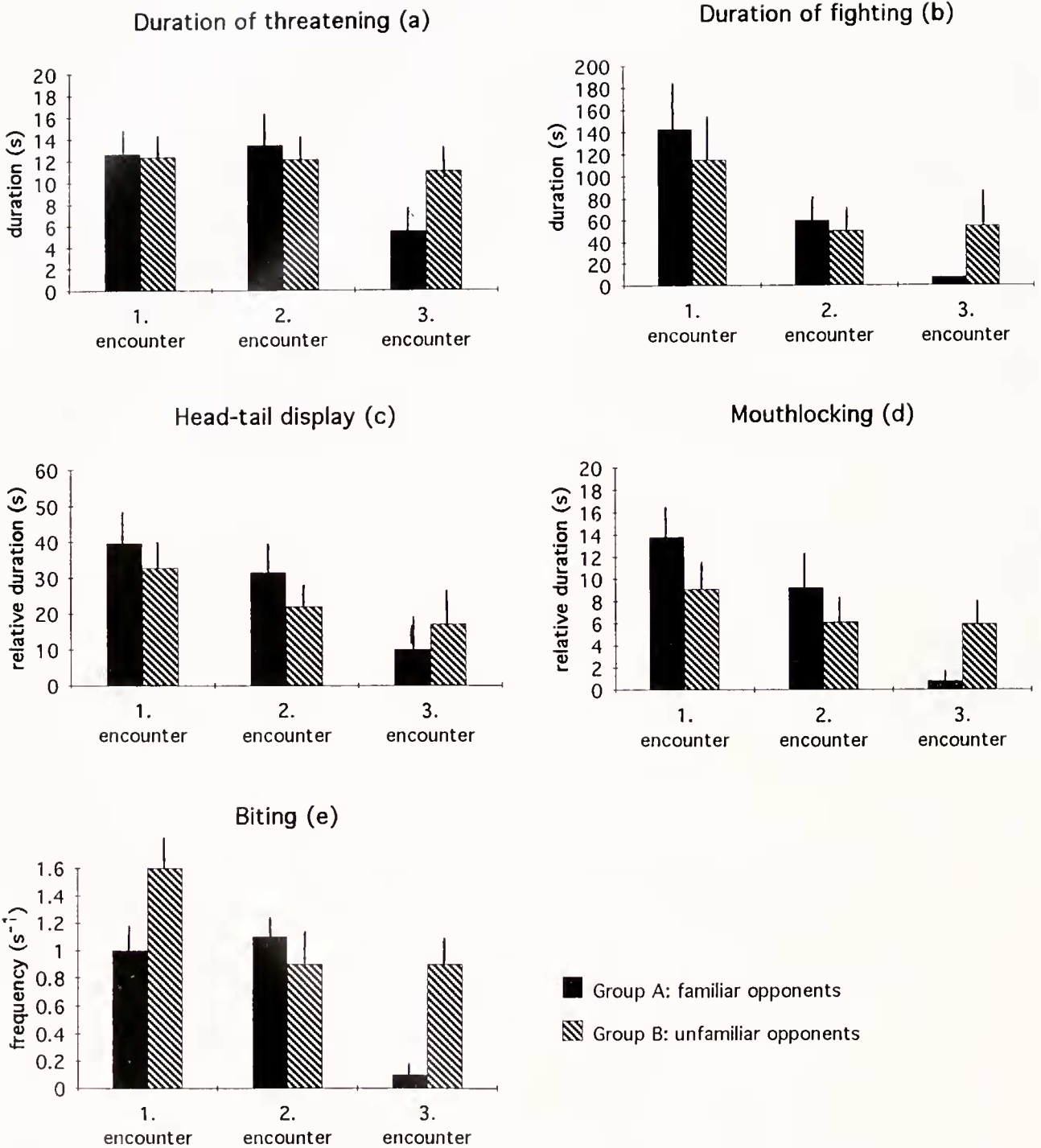
Figure 1. The mean duration of threatening (a) and fighting (b), and the mean relative duration of head-tail display (c) and mouthlocking (d) and biting (e) in the three consecutive encounters of the experimental groups. In group A the opponents were the same for each contest; in group B the former dominant was replaced by a new dominant male for each fight.

were needed to induce significant changes in aggression. On the other hand, repeated encounters with unfamiliar individuals (group B) caused significant changes in only some parameters of fighting. However, the changes that occurred in group B are much less dramatic than those in group A.

The behavior of the contestants was markedly similar during the first two encounters in both groups. This means

that (1) there was no significant change within a group from the first to the second encounter, and (2) behavior did not seem to depend on the familiarity of the opponent during the second encounter. The significant decrease in the duration of fighting can be explained by noting that the first encounter occurred after 3 days of isolation, during which fish could build up energy reserves depleted during the rather long fight (about 2 h on average) at the first encounter (Haller and Wittenberger, 1988; Haller, 1991). Without these energy reserves the second encounter became shorter. However, it is also possible that isolation increased aggression levels.

The defeated fish in group A (same opponents) fought very similarly during the first and second encounters. Although all defeated fish lost the fight again, they gave up fighting only after a considerable time and engaged in both signaling behavior (*e.g.*, head-tail display) and strength-testing behavior (*e.g.*, mouthlocking). The same happened in the group with unfamiliar opponents (B): although defeated fish lost against the formerly dominant opponents, the previous defeat did not seem to change their behavior significantly.

Thus comparing the first two encounters in both groups we find the effect of previous experience on behavior—"status-related memory"—but no direct evidence of social recognition. Since the initial work of Ginsburg and Allee (1942), many studies have documented the effects of prior experience (*e.g.*, Bakker and Sevenster, 1983, Beacham and Newman, 1987). In the case of the paradise fish, defeat decreases the probability of subsequent winning in an aggressive encounter, but prior winning has no influence (Francis, 1983). However, three other factors might decrease the difference between a first and second encounter. (1) Following longer isolation before the first contest (3 days) and between contests (about 22 h), fish fight longer in both the first and second encounters (Miklósi *et al.*, unpub. obs.). (2) The encounter was terminated 1 h after fighting had finished, and fish were fed only following separation, thus opportunities for expressing dominance or submission were limited. (3) The weight symmetry between contestants rendered mutual assessment more difficult, according to the resource holding power (RHP) hypothesis (Parker, 1974). Usually larger animals initiate aggressive encounters and are more likely to win in a shorter fight. Thus similarity in size will increase both the latency of initiation and the duration of a contest.

The third encounter separates the two groups clearly. For fish facing familiar opponents (group A), the duration of the threatening phase decreased by half, and previously submissive fish gave up fighting soon after they began. In contrast, no significant change was observed in the behavior of fish facing unfamiliar opponents (group B). There was about a sixfold difference in biting, mouth-

locking, and duration of fighting between the two groups, which rules out the role of exhaustion. In both groups, submissive fish lost two fights before engaging in the third contest: thus experience in submission or dominance cannot explain the observed difference. As a result, the involvement of some form of social recognition should also be taken into account for the third encounter.

Nevertheless, this experiment does not directly prove that individual recognition takes place. As Waas and Colgan (1994) recently noted, "Individual recognition implies that subjects can distinguish between animals that belong to the same social and physical class." But it is very difficult to tell the exact basis of this form of recognition because individuals can be categorized into several subcategories, and the same animal can use different arrays of variables to categorize its opponents. Because opponents were always of the same social class in both groups (submissive or dominant), the recognition might have occurred on a different level, which suggests that paradise fish are capable of categorization within dominants or submissives. Whether this can be described as individual recognition remains to be seen, and Waas and Colgan (1994) show a good way to examine this subject.

On the other hand, we already have some evidence that individual recognition exists in fish (Gandolfi *et al.*, 1973; Zayan, 1975; Myrberg and Riggio, 1985). For example, as shown by Zayan (1975), individual recognition of formerly dominant fish can reverse the effect of prior residence. Thus, the process of individual recognition interacts with the effects of both prior experience and prior residence in a way similar to that in our present experiment.

It is usually assumed that the end of the fight depends on the decision of the future submissive fish. This idea stems from the classical conditioning view of aggression, in which contact behaviors (biting, mouthlocking) are seen as punishment for the opponent, which learns during the aggressive encounter to avoid these aversive effects (McDonald *et al.*, 1968; Bakker *et al.*, 1989). In this context an individual opponent becomes a conditioned signal for future punishment, but a new opponent acts as a discriminative signal, which does not predict aversive stimulation.

Another theory interprets aggressive encounters in terms of an associative habituation process (Peeke, 1969; Lorenz, 1981). New opponents (or territorial neighbors) disrupt habituation and release an aggressive response. For example, Peeke and Veno (1973) found that resident male sticklebacks attacked unknown territorial neighboring sticklebacks more often than they attacked familiar ones.

The problem of small changes in a complex stimulus, like an opponent, raises a major problem to the incorporation of individual recognition into the learning mod-

els presented above. Either dishabituation or discrimination suppose some form of recognition of the opponent, but we do not know whether this categorization process is similar in the two models or not. As is the case with other processes described mainly on a behavioral level (e.g., imprinting), it is very difficult to explain them in the framework of classical learning models.

At least in paradise fish, it seems that submissive fish try to use every occasion that offers the possibility of winning. Winning a contest presumably has many advantages.

Paradise fish males defend territories and build bubble-nests in shallow waters of rice-fields, where several males breed at the same time near each other (Forselius, 1957). Recognizing neighbors could be advantageous because males spend less time in aggression, leaving time for courtship and later caring for the fry.

Our results support the hypothesis that aggressive experience in the paradise fish influences subsequent aggressive encounters by means of two kinds of memory: one related to the outcome of the encounter ("status-related memory") and the other related to the opponent ("social recognition").

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